Designing a model to investigate cropping systems aiming to control both parasitic plants and weeds

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Abstract

Branched broomrape (*Phelipanche ramosa* (L.) Pomel) is a parasitic plant, which causes severe yield losses in major crops worldwide. Because of its broad host range, including numerous non-parasitic weed species, the persistence of its seeds in the soil, and the poor efficiency of available management techniques, broomrape management is complex. The objective of the present paper was to develop a broomrape-dynamics model to support the design of management strategies combining multiple techniques aiming at long-term control of broomrape. Towards this goal, we developed a simulation model with formalisms and parameters based on data from our own experiments and the literature. This model called PHERASYS combines 1) a demographic submodel to predict broomrape seed bank dynamics, 2) a trophic-relationships submodel to predict the effect of parasitism on crops and weeds, and 3) a submodel of weed dynamics in agroecosystems to predict the growth of crops and weeds from cropping techniques and pedoclimate. Thanks to an individual representation of each host plant, PHERASYS is able to simulate complex heterogeneous canopies. This model can be used as a tool to test management strategies including crop mixtures and relying on biological regulations by weeds.

Keywords: branched broomrape, weed, agroecology, modelling, cropping systems, *Phelipanche ramosa*, PHERASYS, biological regulation

1 Introduction

Broomrapes are parasitic plants that threaten major crops worldwide (Parker, 2013). As holoparasites, they are unable to photosynthesize and entirely rely on host resources to survive (Heide-Jørgensen, 2013). They must germinate close to a host root, after being stimulated by its exudates (Yoneyama *et al.*, 2013), to connect to its vascular system and derive the resources they need (Heide-Jørgensen, 2013). Among broomrapes, branched broomrape, *Phelipanche ramosa* (L.) Pomel, is particularly devastating since it is found on every continent and is able to infect crops in more than 10 botanical families including *Solanaceae*, *Brassicaceae* and *Asteraceae* (Parker and Riches, 1993; Molenat *et al.*, 2013). *Poaceae* species are usually not concerned (Qasem and Foy, 2007; Molenat *et al.*, 2013). In France, it is a major pest of winter oilseed rape, where it can cause up to 90% yield losses (Gibot-Leclerc *et al.*, 2012), and it also infects hemp, sunflower and tobacco (Terres Inovia, 2018).

To date, the only curative method available in arable crops is the application of herbicides on herbicide-resistant crops (e.g, varieties tolerant to imidazolinones) (Fernández-Aparicio *et al.*, 2016a; Données Ephy - Anses, 2018). This approach is used in some countries (e.g., USA) but not available in Europe. Moreover, this technique clashes with current policies aiming to reduce the use of pesticides because of their impacts on human health and environment (Potier, 2014). Most herbicides efficient on broomrape are systemic herbicides such as inhibitors of aromatic (glyphosate) or branched-chain amino acid synthesis (imidazolinones and sulfonylureas) applied to the leaves of the crop (e.g., Eizenberg *et al.*,

2006). To date, none of these are both tolerable to the host plant (with the exception of herbicide-resistant varieties, see above) and lethal to the parasite. Consequently, several preventive techniques with partial effects must be combined to control broomrapes, such as reduced host-crop frequency in the rotation, delayed host-crop sowing or deep tillage (Grenz *et al.*, 2005a; Rubiales and Fernández-Aparicio, 2012; Fernández-Aparicio *et al.*, 2016b). They must provide long-term control because broomrape seeds are assumed to persist up to 20 years in the soil, although this assumption is based on a few studies on species other than branched broomrape (Murdoch and Kebreab, 2013). Moreover, branched-broomrape management must be thought along with non-parasitic weed management (hereafter, the word "weeds" refers to non-parasitic weeds) because several dozens of weed species are hosts (Boulet *et al.*, 2001; Gibot-Leclerc *et al.*, 2003; Simier *et al.*, 2013; Gibot-Leclerc *et al.*, 2015). Weeds might increase broomrape infestation, as they serve as alternative hosts in the absence of host crops. However, they can also deplete the broomrape seed bank, as some species stimulate broomrape germination without supporting further parasite development (Gibot-Leclerc *et al.*, 2003). Such weed species can potentially provide biological regulation of branched broomrape.

As a consequence, branched-broomrape management must be thought at the cropping-system scale, defined by the crop sequence and the techniques implemented in a field (Sebillote, 1990), using multiple techniques and exploiting biological regulations by weeds. Such strategies are complex and require specific tools for decision support. The field experimental approach, for example, is insufficient, since it allows to test only a limited number of techniques, in a few pedoclimatic and floristic contexts for a few years (Jeuffroy *et al.*, 2014).

Simulation models are complementary tools to design cropping systems because they allow evaluating cropping-system performances in the long term in various pedoclimatic and floristic contexts (Bergez *et al.*, 2010; Colbach *et al.*, 2014a; Colbach *et al.*, 2017). Several models of broomrape dynamics have been developed to date which include the effects of cropping techniques on multiannual parasite dynamics (Schnell *et al.*, 1996; López-Granados and García-Torres, 1997; Regan *et al.*, 2011). However, these models usually consider only one crop species, disregard interactions with weather and weeds and do not represent the host plant's root system (i.e., the host's organ on which the parasite attaches). The one notable exception is the model developed by Grenz et al. (2005a). Their model was, though, parameterized for another broomrape species, *Orobanche crenata*, and does not take into account interactions with weeds. A first attempt to adapt it to *P. ramosa* was made with the PHERASYS model (for *Phelipanche ramosa* in cropping systems) (Colbach *et al.*, 2011). It integrated the interactions with weeds thanks to a connection with FLORSYS, a model simulating the dynamics of multispecies weed floras in agroecosystems (Colbach *et al.*, 2014a; Colbach *et al.*, 2021). However PHERASYS remains largely based on the model developed by Grenz *et al.* (2005a), with most parameter values borrowed from *O. crenata*, and processes determining interactions with crops and weeds only partially modelled. In particular, PHERASYS does not simulate the effect of parasitism on host growth, and so it cannot predict yield losses due to parasitism, even though the latter is a major criterion when designing cropping systems.

Consequently, the objective of the present study was to develop a model to simulate branched broomrape dynamics in interaction with multiple crop and weed species in agroecosystems. This model was inspired by the existing PHERASYS but parameters were specifically measured for branched broomrape (hereafter simply called "broomrape"), and the formalisms that describe the broomrape life cycle and the interactions with other plants in the field were redesigned. We (1) proposed a structure for the redesigned PHERASYS version, (2) translated the results of experiments set up purposely for this aim into equations to represent biological processes, and (3) completed missing data from the literature. In a companion paper (Pointurier *et al.*, 2021a), we ran simulations with the model to check the consistency of the model with literature, and to evaluate the potential of cropping systems to manage broomrape and weeds in interaction.

2 Materials and methods

This section first describes the general structure of the redesigned PHERASYS model, and then the data and methods used to determine the equations and parameters that constitute the model. The detailed functions and their biological/agronomic meaning are presented in the "results" section.

2.1 Model structure

The structure for the redesigned PHERASYS was based on the structure of FLORSYS which simulates multispecies crop and weed growth and reproduction at a daily time-step and in 3D from cropping system in interaction with pedoclimate (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013; Colbach *et al.*, 2014b; Munier-Jolain *et al.*, 2014; Colbach *et al.*, 2021; Pointurier *et al.*, 2021b). The present paper focuses on the specific formalisms that were added for parasite life-stages and its impact on host plants. Details on the FLORSYS model can be found in section S1 in supplementary material online.

The user provides inputs to characterize the field (daily weather, latitude and soil characteristics), the crops and cropping techniques (with their dates, tools used and options) and the initial weed seed bank (including broomrape and non-parasitic weed species). From these, PHERASYS predicts the number of broomrape individuals at different stages and the biomass of broomrape shoots every day depending on biophysical processes (Figure 1). Each day, a part of the seeds in the soil dies; non-dormant seeds can germinate only if stimulated by neighbouring plant root exudates; the germinated seeds must attach to nearby susceptible plant roots before emerging, flowering and producing new seeds. Attached broomrapes die either when they have finished their life cycle, or when their host dies of old age or is destroyed by cultural operations. PHERASYS also simulates the effect of parasitism on host plant growth.

As FLORSYS, PHERASYS represents the canopy in 3D and discretized with voxels ("3D pixels") whose size (e.g. 4×4×4 cm^3) is chosen by the user. Each non-parasitic plant is represented in 3D, albeit simplified as a cylinder (above-ground) on top a spilled cone (below-ground). The plant's above-ground height, width and leaf area are explicitly located in 3D to simulate competition with neighbouring plants for light. Similarly, the plant's root system is represented in 3D, distributing root length density and biomass across voxels. Broomrape plants are not explicitly represented in 3D, only the location of their host as well as the number and biomass of shoots infecting this host are computed. Seed position in the soil is simulated in a 1D vertical dimension, with 30 successive 1-cm-thick soil layers across which seeds are distributed, with heat and water transfer functions across soil layers. Seeds are assumed to be distributed homogeneously within a soil layer and their future to depend on conditions (temperature, water potential, proximity to host roots) within this soil layer.

2.2 Connections with FLORSYS to model interactions with crops and weeds

PHERASYS was connected to FLORSYS to predict the growth of crops, non-parasitic weeds and soil conditions from cropping system components and pedoclimate (Figure 1). PHERASYS and FLORSYS connect two ways, with variables from FLORSYS influencing broomrape dynamics in PHERASYS, and variables from PHERASYS driving the effect of parasitism on host growth in FLORSYS.

Soil temperature and moisture (which are predicted from weather, soil characteristics and management techniques, Brisson *et al.*, 2003) determine dormancy relief of broomrape seeds and germination progress. The root volume of host plants determines the probability that parasitic seeds encounter roots that stimulate them and support their subsequent attachment. Host biomass determines the amount of resources available for broomrapes and thus the number of broomrapes the host can potentially support. Host phenology determines when root exudates that trigger broomrape germination are released and when attached broomrapes start to grow from host resources. Host growth, which is driven by wphotosynthesis and respiration processes in FLORSYS, is reduced by parasitism. Biomass allocation between roots and above-ground organs is also modified due to parasitism.

Effect of tillage on broomrape-seed movements in the soil is simulated by the seed-movement submodel of FLORSYS (see principle in Gardarin *et al.*, 2012). Any effect of cropping technique on host plants in FLORSYS indirectly affects broomrape dynamics in PHERASYS since it results in host mortality or host

biomass reduction (e.g., effect of herbicides on weed) or host biomass increase (e.g., weed management reduces competition with crops).

2.3 Data origin

2.3.1 Published data

The first simplistic PHERASYS version pointed out gaps in knowledge of broomrape biology (Colbach *et al.*, 2011). Experiments were set up to study and quantify insufficiently known processes, i.e. seed mortality, dormancy and production of the parasite as well as host-parasite trophic relationships. Most results were published (see [1] in Figure 1) and are summarized in Table 1. The experiment quantifying broomrape seed production was described in the present article (see [2] in Figure 1 and section2.3.2). Further data was taken from experiments carried out by other teams (see [3] in Figure 1).

Branched broomrape consists of several pathovars i.e. genetically distinct populations with different host preferences (Brault *et al.*, 2007). Our study focussed on the pathovar predominant in oilseed rape which causes the main damages in France (Terres Inovia, 2018). When no data on this pathovar were available, data on other pathovars were used instead (Appendix A 4).

2.3.2 Measuring broomrape seed production

Broomrape at fructification stage were collected in July 2017 in two oilseed rape fields infested with broomrape in Fontenay-le-Comte (46°26'44" N, 00°46'09" W; Vendée, France) and Saint-Ouenne (46°25'44" N, 00°28'04" W; Deux-Sèvres, France) at crop harvest. Each broomrape consisted of a stem possibly bearing several branches. In total, 36 broomrapes were collected. They were split into two samples to estimate (1) the mean number of seeds produced per seed capsule (structure containing seeds in broomrapes) on six broomrapes (three from each field), and (2) the number of capsules produced per broomrape on the 33 remaining broomrapes.

In the first sample, closed capsules (still comprising their seeds) of each broomrape were counted and dried for 48 hours at 80°C. Then, they were opened to collect the seeds. Seeds and empty capsules were weighted separately. The number of seeds was counted under a stereoscopic microscope (1.95x – 250x). Some capsules could not be opened because they were atrophied, contained immature seeds (black seeds that stayed attached in the capsule), or seeds had been eaten by insects (with insect or larvae still inside the capsule). They were counted and weighed separately.

In the second sample, the number of capsules was counted on each broomrape, discriminating closed, empty (having already released their seeds) and missing capsules (leaving an abscission mark on the stem). Closed capsules and broomrape stems from which capsules had been removed were dried for 48 hours at 80°C and weighted separately.

In samples collected in Fontenay-le-Comte, broomrapes were counted on each host to analyse the trade-off between number of broomrapes attached on a host and the biomass of each broomrape. Biomass per broomrape was calculated as the total biomass of broomrapes (including stems, open and closed capsules) collected on a given host, divided by the number of broomrapes attached on this host. Since the open capsules had not been weighed in the second sample, the mean open capsule weight measured in the first sample was used instead and multiplied by the number of opened capsules counted.

2.4 Statistical analysis

Data from published data (section 2.3.1) and from the field samples (section 2.3.2) were analysed using R (R Core Team, 2019). Linear models were fitted with the R package "lm" and non-linear models with "nls" and "nls2" of R. The algorithm "brute-force" was used to solve cases of failed convergence with function "nls2". A pseudo-R^2 was calculated to estimate the predictive quality of non-linear models (UCLA: Statistical Consulting Group, 2015).

3 Results

3.1 Modelling broomrape dynamics

The following subsections describe how the redesigned PHERASYS models the different stages of the broomrape life-cycle and which data and hypotheses were used. The detailed equations can be found in Appendix A 1, Appendix A 2 and Appendix A 3.

3.1.1 Seed mortality in the soil

Broomrape life-cycle starts in the soil as a seed. Some seeds die due to aging, diseases or predation resulting in annual seed bank decline of 7% (eq. [1] in Appendix A 1) (Pointurier *et al.*, 2019). This annual mortality rate was converted into a daily rate using the same equation as in FLORSYS for non-parasitic weeds (Gardarin *et al.*, 2012).

3.1.2 Seed dormancy

Fresh broomrape seeds are dormant. They require (1) a period of dry storage, followed by (2) a period of moist storage ("conditioning"), and finally (3) a stimulation by root exudates of potential host plants to relieve dormancy. In field conditions, seed dormancy varies moreover with the season (Murdoch and Kebreab, 2013). Dormancy was modelled as two successive phases in PHERASYS: (1) dormancy relief of new seeds, as a function of soil temperature and moisture; and (2) seasonal dormancy, as a function of time since seed shed.

According to data from Gibot-Leclerc et al. (2004), once moisture requirements are met (≥ -2MPa), dormancy relief of fresh seeds depends solely on temperature during the conditioning period (section **S1** in supplementary material online). No seed germinates if temperature during conditioning is too cold or too hot (< 0°C or > 37°C, even if temperature during exposure to root exudates are adequate). In-between these temperature thresholds, the closer the temperature is to the optimum, the faster the seeds lose dormancy (section **S1 online**). Thus, the proportion of non-dormant seeds among viable seeds was modelled as a function of thermal time accumulated during conditioning using a Weibull equation (eq. [3] in Appendix A 1, Figure 2). Thermal time is calculated in each soil layer as a function of soil temperature and cardinal temperatures of conditioning [2] (equation adapted from Bradford, 2002). The latter were calculated with the method for calculating cardinal temperatures for germination (Bradford, 2002).

Older seeds (but still younger than one year) follow a seasonal pattern of dormancy, with a high dormancy (> 80% dormant seeds) in winter-spring and a low dormancy (< 10% dormant seeds) in summer-autumn (Pointurier *et al.*, 2019). Seeds older than one year enter dormancy two months later. This seasonal dormancy was modelled as a function of seed age [4], using the same equation as for non-parasitic weeds (Gardarin and Colbach, 2015).

3.1.3 Stimulation of germination

Dormancy relief ends with germination triggering by root exudates of plants. The stimulatory activity of root exudates depends on the species emitting them (Fernández-Aparicio *et al.*, 2009; Gibot-Leclerc *et al.*, 2016; Perronne *et al.*, 2017). Data from germination tests from the literature were compiled to calculate the ability of crop and weed species to stimulate broomrape relatively to GR24, a synthetic stimulant commonly used as a synthetic control (Mangnus *et al.*, 1992) (Appendix A 4). This method allowed us to compare data from different experiments. When experiments did not include GR24 but oilseed rape as a positive control, the ability of the species to stimulate broomrape was first calculated relatively to oilseed rape, and then multiplied by the ability of oilseed rape to induce germination relatively to GR24. When no data were available for a species, its ability to stimulate broomrape germination was estimated from a close species (e.g., the data of *Medicago lupulina* were used for *Medicago sativa*). When no data on broomrape germination were available, the number of broomrapes attached per plant relative to a sensitive species (e.g. oilseed rape, tomato or *Geranium dissectum*) was used instead. If absolutely no data could be found in the literature, the species was considered to be unable to stimulate broomrape germination.

Broomrape seeds must be close to a stimulating root to be able to perceive germination stimulants (≤ 36 mm, Goldwasser and Yoder, 2001). So, every day in PHERASYS, a part of the non-dormant seeds are stimulated (eq. [6] in Appendix A 1), corresponding to the proportion of soil volume comprised in the "stimulating zone" [5], i.e. close enough to stimulating roots (section **S2** online). As root exudates are mainly released at root tips (Brown and Edwards, 1944; Dennis *et al.*, 2010), broomrape seeds are only stimulated by the "new" stimulating zone predicted each day, i.e. the stimulating zone on the present day minus the one from the day before [6]. Plants are considered to be able to induce germination from emergence to the end of flowering (Auger *et al.*, 2012), which is also approximately the time when plants stop emitting new roots (Gregory *et al.*, 1995).

3.1.4 Germination progress

Once stimulated, seeds start to germinate. The wetter and the warmer the soil layer is (i.e. the higher above base temperature and base water potential, Bradford, 2002), the faster the seeds germinate (Pointurier *et al.*, 2019). Germination dynamics of broomrape seeds are simulated using the same principle as Gardarin *et al.* (2011), i.e. as a function of hydrothermal time accumulated since germination triggering by root exudates (eq. [7] in Appendix A 1). Too cold temperatures (below base temperature) halt germination temporarily. When the soil is too dry (i.e. below base water potential), or after a tillage operation which dilutes root exudates in the soil, germination stops altogether and new root exudates are necessary to trigger germination again [8]. Base temperature and base water potential of germination were taken from Gibot-Leclerc *et al.* (2004) (section **S1** online), and germination dynamics parameters from Pointurier et al. (2019).

Every day, germination flushes are triggered by new stimulating roots in the model. Consecutive flushes are merged to avoid storing data from several simultaneous germination flushes in the computer memory. To avoid large under or overestimation (see details in section **S3** online), only close enough flushes (i.e. the new flush occurs before the ongoing flush has run 2.5 times its time to mid-germination) are merged. Otherwise, only the most recent flush is kept [7].

Germinated seeds are removed from the seed bank daily [9].

3.1.5 Attachment

Germinated seeds produce a radicle which grows towards the host root to attach and establish vascular connections to take up water and nutrients from the host (Joel, 2013b). Yet not all species that stimulate broomrape germination also support broomrape attachment. The ability of a species to allow broomrape attachment after stimulation and consecutive development was compiled from the literature (Appendix A 4). Radicle elongation is limited, so only germinated seeds within a 4 mm "attachment zone" around host roots and younger than three days can attach, otherwise they die (Gibot-Leclerc *et al.*, 2012).

First, the volume of the attachment zone is calculated for each host plant (eq. [10] in Appendix A 1) and cumulated over all host plants to determine the proportion of soil volume where broomrape seeds are close enough to host roots to attach, and to deduce the total number of broomrape attachments [11]. Then, attachments are distributed over the hosts proportionally to their contribution to the total attachment zone [12].

3.1.6 Survival on the host

Only a few attached broomrapes survive on the host until flowering (Moreau *et al.*, 2016), depending on the biomass the host allocates to them (Figure 3) (Grenz *et al.*, 2005b; Lins *et al.*, 2007; Grenz *et al.*, 2008). Host biomass at rosette stage represents a potential biomass to be used by broomrapes since, at this stage, parasitism has not yet an effect on host biomass (Moreau *et al.*, 2016). Above a minimum host biomass threshold, the total number of emerged broomrapes per host plant increases linearly with increasing host biomass at rosette stage. Hosts whose biomass is below the threshold do not have enough biomass to support the growth of emerged broomrapes.

The relationship of Figure 3 was used to calculate host carrying capacity in PHERASYS (eq. [13] in Appendix A 1). Moreover, this capacity is limited to a maximum of 20 broomrapes per host plant in our model, which corresponds to the maximum number of broomrapes observed per oilseed rape plant in

heavily infested fields (Gibot-Leclerc *et al.*, 2012). The host-carrying capacity allows introducing density-dependence into the model, i.e. the more broomrapes compete on a host, the less likely each of them is to survive. To represent this, we adapted a relationship used to simulate intra-specific competition between oilseed rape seedlings for emergence (Colbach *et al.*, 2001). This relationship [15] calculates the number of emerged broomrapes from the number of (unemerged) broomrapes attached at host rosette stage [14], when host-carrying capacity is determined [13]. Since broomrape can still attach after host rosette stage, the competition relationship [15] was derivated to calculate the survival probability for broomrapes attached daily after rosette stage [16]. The surviving emerged broomrapes are summed until broomrape reproduction [17]. They may though die before reaching seed production if the host dies earlier due to old age, frost or management operations (harvest, herbicide, tillage etc) [18].

3.1.7 Broomrape biomass

Broomrape phenology is predicted solely from temperature, since it does not depend on host phenology (Gibot-Leclerc *et al.*, 2013a), year or experimental conditions (fields or greenhouse) (Gibot-Leclerc, 2004). So, once attached, broomrape biomass accumulation is simulated from thermal time since host emergence (eq. [20] in Appendix A 1). Broomrape biomass becomes noticeable at about 700°C·days (base 5°C) after host emergence (Figure 4). The maximum biomass that the broomrapes can derive from the host is reached approximately at double this time, and 50% of this maximum biomass is reached after about 1100 °C·days [21].

This maximum biomass depends on the number of emerged broomrapes competing with each other for resources on the same host at the end of their life cycle (see section 3.1.6). The more emerged broomrapes survive on a host, the less biomass is available for each of them [19] (Hibberd *et al.*, 1998; Grenz *et al.*, 2005b; Mauromicale *et al.*, 2008; Fernández-Aparicio *et al.*, 2016a; Moreau *et al.*, 2016) (Figure 5). The later intraspecific-competition relationship was parameterized from data from the greenhouse experiment of Moreau et al. (2016) and not from our field measurements (section 2.3.2) because data from Moreau et al. (2016) presented a larger range of values (on the x-axis, Figure 5). However, our field measurements are consistent with data from Moreau et al. (2016) (Figure 5).

3.1.8 Seed production

Assuming that broomrape phenology is mainly driven by temperature (see section 3.1.7), broomrape seed production occurs at 1709°C·days (base 5°C, section **S4** online) after host emergence in the model, whatever the host, the location or the cropping system (eq. [20] in Appendix A 1).

Our measurements (section 2.3.2) on broomrape reproduction demonstrated that the number of capsules containing seeds increased linearly with broomrape biomass (Figure 6), while seed biomass per capsule (0.55 ± 0.082 mg) and individual seed biomass (2.1 ± 0.26 µg) were relatively constant. A small proportion (8%) of the analysed capsules did not produce mature seeds as they were either eaten by insects, atrophied or did not have the time to reach maturity. As a result, the model calculates broomrape seed production by (1) calculating the number of capsules from broomrape biomass and the proportion of unproductive capsules, (2) multiplies the capsules by their average seed weight to get seed biomass, (3) divides it by average seed weight to obtain the number of broomrape seeds per host plant, and (4) multiplies it by seed viability in fresh seeds to produce the number of viable broomrape seeds [22]. The seed viability (0.93 seeds·seeds^{-1}) was measured in a previous experiment (Pointurier *et al.*, 2019).

Finally, seeds are released and added to the surface layer of the broomrape seed bank [23].

3.2 Modelling the effect of parasitism on host growth

The following subsections describe the effect of parasitism on host growth and reproduction as well as the data used to justify and fit the equations. As host phenology is not affected by parasitism (Gibot-Leclerc *et al.*, 2013b; Moreau *et al.*, 2016), the relevant equations used by FLORSYS (Colbach *et al.*, 2014b) remain unchanged.

3.2.1 Pathosystem biomass loss

The model considers broomrape as a supplementary sink for the host (Manschadi *et al.*, 2001; Grenz *et al.*, 2008; Fernández-Aparicio *et al.*, 2016a) and simulates the total pathosystem biomass consisting of both the host and the attached broomrapes. The amount of biomass lost by infected hosts is not fully invested in broomrapes, resulting in a reduction of the pathosystem biomass compared to the biomass of healthy plants (Barker *et al.*, 1996; Eizenberg *et al.*, 2005; Lins *et al.*, 2007; Grenz *et al.*, 2008; Moreau *et al.*, 2016). Up to host flowering, parasitism has little or no effect on the pathosystem biomass (Moreau *et al.*, 2016). Then, broomrape starts to emerge and reduces the pathosystem biomass by 27 % (Figure 7). This loss rate is applied in our model to the daily net biomass produced after photosynthesis and respiration predicted in FLORSYS (eq. [24] in Appendix A 1).

3.2.2 Reallocation among vegetative organs

Before rosette stage, parasitism has no effect on the proportion of the pathosystem biomass allocated to roots (p=0.67). After that key stage, it reduces the root to pathosystem biomass ratio by 21% (Figure 8). Biomass allocation to roots is reduced accordingly in PHERASYS (eq. [25] in Appendix A 1). Biomass allocation to leaves in the pathosystem is not affected by parasitism (Moreau *et al.*, 2016), so the FLORSYS equations determining the leaf biomass ratio remain unchanged (Colbach *et al.*, 2014b) [26].

3.2.3 Host seed production

Since broomrape competes mostly with the reproductive compartment of the host (Manschadi *et al.*, 2001; Grenz *et al.*, 2008; Fernández-Aparicio *et al.*, 2016a; Moreau *et al.*, 2016), the combined biomass of broomrapes and host reproductive organs (flowers and fruits) was compared to the biomass allocated to reproduction in healthy host plants (Figure 9). In healthy host plants, a part of the above-ground biomass is allocated to seeds (Colbach *et al.*, 2014b) (eq. [27] in Appendix A 1). In infected hosts, this part, together with broomrape biomass, is 1.7 times higher [28]. In the model, the biomass allocated to host seeds in infected hosts is computed by subtracting the broomrape biomass (calculated in section 3.1.7) from the biomass allocated to host reproduction and broomrapes [29]. Although host plants did not reach full maturity in the data we used from Moreau et al. (2016), we considered that our formalisms were still valid at later stages because the proportion of above-ground biomass allocated to the reproductive compartment varies only little then (Weiner, 2004).

This formalism takes into account that hosts that reproduce early suffer less from broomrape competition (Manschadi *et al.*, 2001; Grenz *et al.*, 2005b; Moreau *et al.*, 2016) (section **S5** online).

3.3 Effect of host-plant phenology on host-parasite interactions

Host-plant phenology (which discriminates five stage: cotyledon, plantlet, vegetative, flowering, maturation, see details in section S1.4 online) influences parasite growth and reproduction as well as the impact of parasitism on host growth and reproduction, as seen in the previous section. In summary:

- Host-plant emergence determines the onset of root emission and growth, which sets off host-root exudation triggering parasite germination as well as parasite attachment to host roots;
- When a host plant reaches the "rosette" stage (approximately 25% of the duration of its vegetative stage), the parasite starts to affect host growth and biomass allocation to different plant compartments;
- When a host plant starts to flower, biomass allocation to roots slows down and stops, which shuts off host-root exudation (and the resulting parasite germination) as well as parasite attachment to host roots;
- The duration of the host's life cycle determines whether the parasite has the time to reproduce but the time from parasite emergence to parasite maturity does not depend on the host plant.

3.4 Modelling the effects of cropping systems on broomrape dynamics

The different processes modelled in PHERASYS allowed integrating the effects of several cropping techniques (Table 2). For example, soil tillage moves seeds in the soil, which makes them more or less close to stimulating root exudates and to host roots and thus determines the number of stimulated broomrape seeds and attachments.

4 Discussion

4.1 The first cropping-system model of broomrape dynamics specific to branched broomrape…

The redesigned PHERASYS is the first model of broomrape dynamics in agroecosystems specifically designed and parameterized for branched broomrape. The life-stages chosen as key steps to model broomrape dynamics are basically the same as those included in other models (Schnell *et al.*, 1996; López-Granados and García-Torres, 1997; Eizenberg *et al.*, 2005; Grenz *et al.*, 2005a; Ephrath and Eizenberg, 2010; Pérez-de-Luque *et al.*, 2016). However, seed dormancy was rarely included in previous models and when it was, this was done very simplistically (i.e., a constant proportion of the seed population was considered to be dormant, López-Granados and García-Torres, 1997; Grenz *et al.*, 2005a). We modelled dormancy more precisely as two successive phases. First, dormancy relief in fresh seeds depended on temperature, moisture and duration of conditioning. Kebreab and Murdoch (1999) used a similar approach to model both dormancy release and induction of seeds in other broomrape species under laboratory conditions. We preferred using a seasonal, more realistics model for older seeds, built from a field experiment. This approach was shown to produce satisfactory predictions in non-parasitic weeds (Colbach *et al.*, 2016).

Some PHERASYS formalisms were inspired from the model developed for *O. crenata* (Grenz *et al.*, 2005a), e.g. the calculation of the "stimulating zone" around roots and the estimation of broomrape seed production. Here, we not only estimated parameter values for branched broomrape, we also improved the initial concepts. For instance, we added a dynamic and more realistic approach to the stimulating zone by restricting it to root tips. As Grenz *et al.* (2005a), we found that the number of seed-containing capsules was related to broomrape biomass. From this relationship, we estimated that each broomrape produces 10000 to 55000 seeds, which is at the lower end of the range of 10000 to 500000 seeds reported for other broomrape species in the literature across different continents (Grenz *et al.*, 2005a, Turkey; Joel, 2013a; Prider, 2015, Australia). However, our mean number of seeds per capsule (200-300) was lower than the 500-700 seeds generally found in broomrapes, including branched broomrape (Gibot-Leclerc *et al.*, 2012; Joel, 2013a; Prider, 2015). Indeed, because of experimental constraints, our measurements of seeds per capsule only included the closed capsules from the top of the inflorescence, which contain fewer seeds (Miegel *et al.*, 2013). If future sensitivity analyses demonstrate that this parameter is essential for predicting branched-broomrape dynamics and the resulting yield loss, we will carry out additional measurements with an improved protocol.

We used the well-known concept of thermal time (Bonhomme, 2000) to predict broomrape phenology, which had already been successfully applied to several other broomrape species (Eizenberg *et al.*, 2005; Eizenberg *et al.*, 2009; Ephrath and Eizenberg, 2010; Eizenberg *et al.*, 2012a; Eizenberg *et al.*, 2012b; Pérez-de-Luque *et al.*, 2016; Hosseini *et al.*, 2017). Using this concept here involved assuming that broomrape phenology depends mostly on temperature and not on host phenology. This assumption was supported by observations on *O. crenata* (Manschadi *et al.*, 2001; Grenz *et al.*, 2005b) as well as field observations on branched broomrape (Gibot-Leclerc *et al.*, 2012).

4.2 … in interaction with several species of crops and weeds …

The major originality of PHERASYS consists in the interactions between broomrape and several species of crops and weeds. At present, more than 60 species are included in the model and its generic structure makes it easier to add new species in the future (Colbach *et al.*, 2021). Broomrape dynamics models in the literature include generally only one host crop, three to four at the most (Schnell *et al.*, 1996; Pérez-de-Luque *et al.*, 2016), and no weed species.

We characterized parasite interactions with crops and weeds at the individual host plant level by predicting the number of germinated broomrape seeds, attachments and mature broomrapes as a function of daily host biomass and root volume. This allowed modelling, for the first time, the effects of heterogeneous multispecies stands on broomrape dynamics. For example, our model takes into account the fact that hosts located close to germination-stimulating non-attaching plants are more infected, or

that shaded hosts are less infected. This is crucial for designing management strategies using biological regulation by either weeds or crop mixtures associating complementary species.

Our species parameters need, though, to be improved. First, the stimulatory activity of species was estimated from *in vitro* germination tests. It is likely to be different in the field since seasons (López-Granados and García-Torres, 1996; Fernández-Aparicio *et al.*, 2014), nutrient availability (Gaudin, 2013) or interactions with microorganisms (Fernández-Aparicio *et al.*, 2010) may influence the stimulatory plant activity. Moreover, data from a related species or from other broomrape pathovars were used to parameterize some species. This is acceptable for *Fabaceae* (Perronne *et al.*, 2017), but not for *Brassicaceae* where similar species induce different responses in branched-broomrape germination which also depend on the broomrape pathovar (Gibot-Leclerc *et al.*, 2016). Even with such proxys, some species known to stimulate branched broomrape could not be parameterized for stimulatory activity (e.g., *Fallopia convolvulus*, Boulet *et al.*, 2007) and were considered as non-host. Misestimating the stimulatory activity of a species can result in misestimating broomrape seed bank depletion due to germination losses and/or broomrape reproduction due to successful germination and attachments. Future sensitivity analyses will identify which model parameters should be measured as a priority.

4.3 … and including a submodel for host-parasite trophic relationships

Another novelty of PHERASYS is that interactions between broomrape and host plants are two-ways, i.e. host plants have an effect on broomrape dynamics while parasitism influences host growth. This allows estimating yield losses due to parasitism and improves the prediction of plant-plant competition for light and other resources in FLORSYS. Broomrape dynamics are also better predicted, via a feedback loop, as host growth and biomass determine broomrape infestation in PHERASYS.

Grenz *et al.* (2005a) also included a submodel for host-broomrape trophic relationships as we did here, but on a different broomrape species and with a single host species in homogeneous stands. Grenz et al's model focused more on within-plant variability on an average host plant; for instance, parasitism caused abortion of young fruits whereas older, more competitive fruits survived. We included little within-plant variability of broomrape effects, only considering that late broomrape attachments rarely survived, in order to focus on between-plant variability. This 3D individual-based representation of each host (and non-host) plant was better adapted to the multispecies nature of FLORSYS and still allows modelling the competitive advantage of hosts reproducing early.

Although most formalisms that we proposed here to model host-broomrape trophic relationships are new, the concepts involved are supported by the literature (see references in the result section). Some less well-known properties emerged from our work and also found support in the literature. For example, broomrape affects the allocation of resources within host vegetative organs before deriving biomass (Barker *et al.*, 1996), reducing the allocation to roots in the pathosystem (Lins *et al.*, 2007). However, our formalisms were based on data from only three host species and need to be checked on more species since they may vary between hosts (Fernández-Aparicio *et al.*, 2016a).

4.4 Agronomic implications

The structure of the FLORSYS-PHERASYS model complex makes it possible to simulate a large range of contrasting cropping systems, including both direct effects on the parasite (e.g., tillage influences broomrape-seed movements) as well as indirect effects via the crop and non-parasitic weeds (e.g., plant species, host plant location and biomass, triggering of suicide broomrape germinations), and this in interaction with pedoclimate (e.g., parasite attachment success also depends on soil temperature and water potential). Thus, the effects of cropping techniques potentially efficient for controlling broomrape can be evaluated, sometimes resulting from a combination of underlying processes (Table 2). Promising techniques such as trap and catch crops aiming to deplete the soil seed bank, delayed sowing or reduced host crops frequency in the rotation aiming to limit broomrape reproduction can be evaluated indidivudally in terms of broomrape control in various weather scenarios. More importantly, combinations of individual techniques can be evaluated and fine-tuned to fit to different pedoclimates, weed-flora contexts or cropping-system types.

The model will also allow investigating how to exploit interactions between broomrape and non-parasitic weeds for biological regulation of broomrape. Though weeds can allow broomrape to reproduce as shown in our previous experiments (Moreau *et al.*, 2016), these same experiments illustrate that non-parasitic weeds can potentially play the role of catch plants. Indeed, some weed hosts have a shorter life cycle than broomrape and thus preclude seed-bank replenishment after triggering broomrape germinations. This effect will though be highly dependent on the quality of the weed phenology predictions in FLORSYS, which was shown to be deficient at some latitudes (Colbach *et al.*, 2016).

4.5 Perspectives

The previous discussion advertises the many potential uses of PHERASYS. In addition to investigating the effects of cropping techniques, a sensitivity analysis to model parameters would allow identifying the key processes in broomrape dynamics and, incidentally which model parameters need to be measured more precisely and which formalisms must be improved.

To extend the range of broomrape-controlling strategies, more management techniques could be included in the model, such as parasite-tolerant crop varieties, fertilization or biological control with fungi and insects. The process-based modular structure of PHERASYS facilities the addition of techniques and processes, providing that data for parameterization are available. For example, techniques having a direct toxic effect on broomrape, such as herbicides, could be modelled by eliminating a part of the broomrape population when applied. Indirect effects influencing root exudation, such as fertilization (Fernández-Aparicio *et al.*, 2016b), would modulate the stimulatory activity of plants. PHERASYS also benefits from FLORSYS improvements. Now that competition for nitrogen has been included in FLORSYS (Moreau *et al.*, 2021), we will be able to investigate how fertilization strategies could be adapted to make hosts more competitive towards broomrape.

Finally, as suggested above, processes modelled in PHERASYS are quite generic. The same model structure can be used for other pathovars of branched broomrape or other broomrape species, albeit with different parameter values. We started to collect parameter values for the hemp pathovar (Appendix A 4), which is the second most frequent in France (Terres Inovia, 2018).

5 Conclusion

We developed PHERASYS, a mechanistic model of broomrape dynamics in agroecosystems, specifically designed and parameterized for branched broomrape. It allows, for the first time, to simulate interactions between broomrape and heterogeneous multispecies stands of crops and weeds. It integrates the effects of multiple cropping techniques, including complex ones playing on the competition between broomrapes and hosts for resources. The next step will be to determine how to combine partially efficient cropping techniques into a consistent cropping system to control broomrape harmfulness and, in particular, how to manage non-parasitic weeds in order to contribute to biological regulation of broomrape.

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8 Illustrations

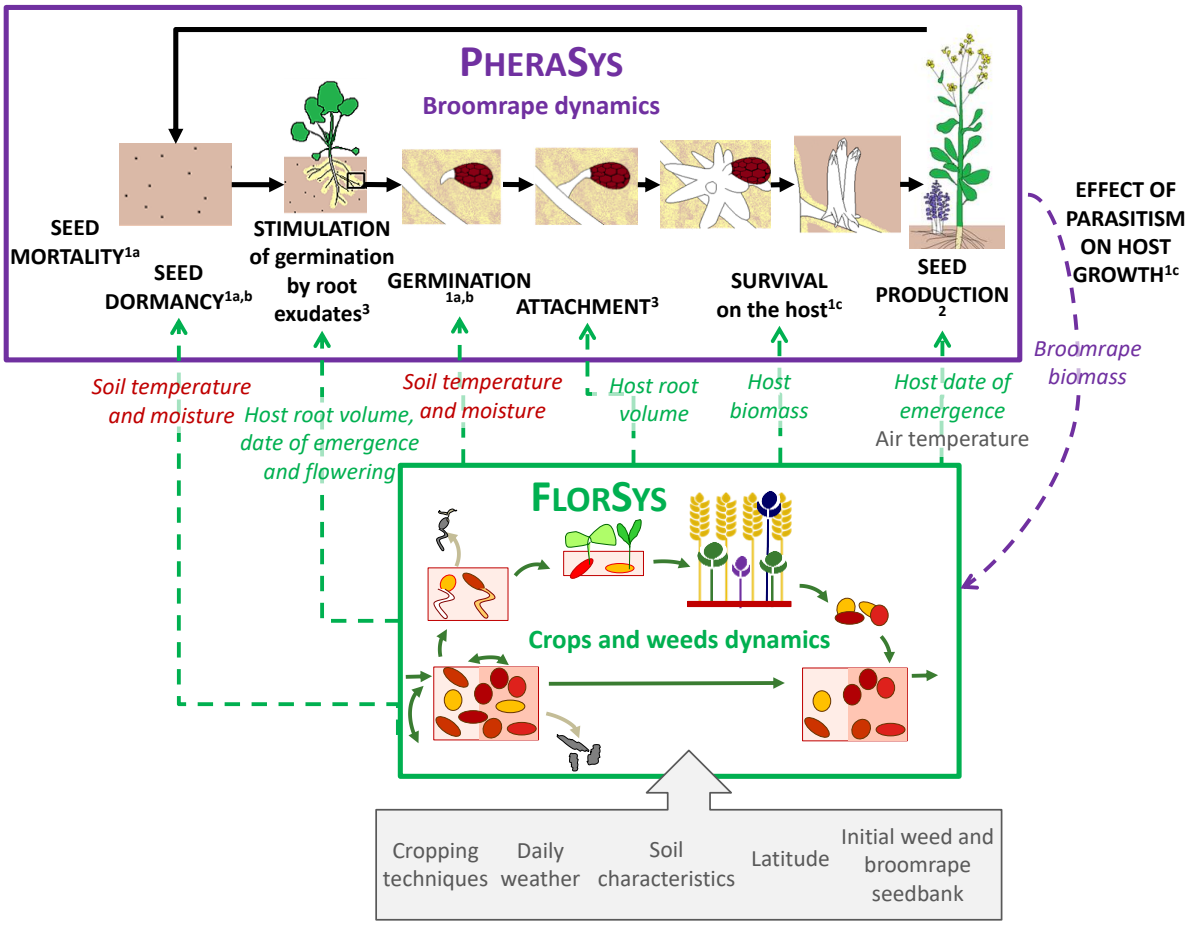

Figure 1: Processes of branched-broomrape life cycle modelled in the redesigned PHERASYS model (in bold, section2.1) and connection with FLORSYS. Inputs given by the user are in grey. Variables used to connect both models are in italics (section 2.22.2; green and purple: biotic variables from FLORSYS and PHERASYS respectively, brown: abiotic variables). Numbers indicate the origin of the data used with [1]own data published ([1a]Pointurier et al. (2019), [1b]Gibot-Leclerc et al. (2004), and [1c]Moreau et al. (2016), Table 1), [2]experiment described in the present article (section 2.3.2) and [3]other literature (Olivia Pointurier 2019)

Table 1: Summary of own published data working with Oilseed rape pathovar (Brault *et al.*, 2007; Le Corre *et al.*, 2014) used to build and parameterize PHERASYS

Data	Experimental conditions	Treatment	Measures
Gibot-Leclerc *et al.* (2004)	Germination on glass microfibre paper *in vitro*	Different durations of conditioning at different temperatures and water potentials	Proportion of germinated seed after stimulation with GR24 (synthetic growth regulator used to stimulate broomrape germination)
Moreau *et al.* (2016)	Co-cultivation of branched broomrape with hosts in pots in greenhouse	3 hosts species (*Brassica napus*, *Capsella bursa-pastoris*, *Geranium dissectum*) grown under 3 light conditions in substrate heavily infested with broomrape seeds or uninfested and harvested at 4 phenological stages	Biomass of broomrape and host organs and number of attached broomrapes.
Pointurier *et al.* (2019)	Seeds buried in the field and put to germination on glass microfibre paper in vitro	Germination after different durations of burial in the soil up to 2 years	Proportion of viable and germinated seeds after different durations of burial and stimulation with GR24

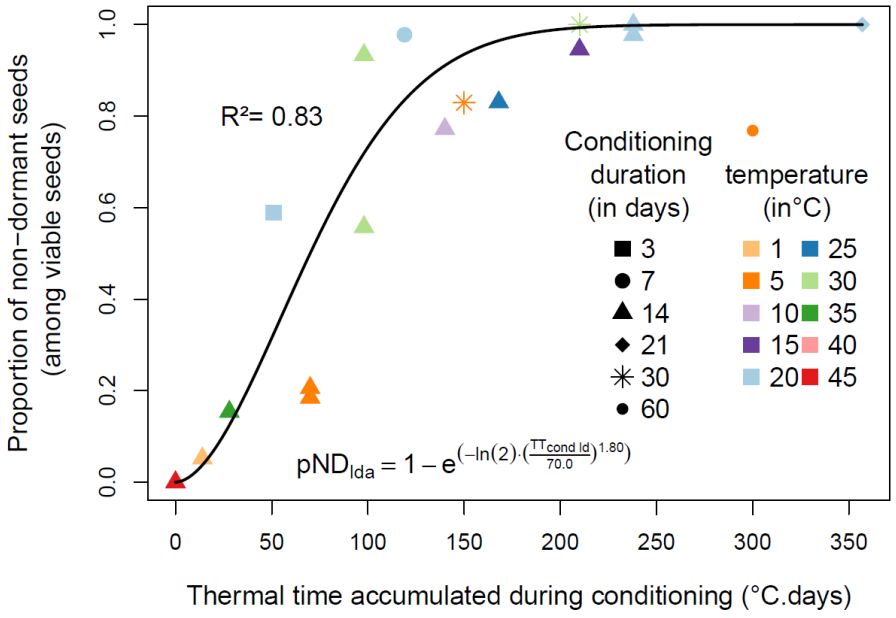

Figure 2: Dormancy relief of branched-broomrape seeds as a function of thermal time accumulated during conditioning ($TT_{cond\ ld}$, base 0°C). Each dot represents the proportion of seeds (pND_{ld}) germinating after being stimulated with a synthetic stimulant (GR24 at 1 $mg.L^{-1}$ at 20°C, i.e. optimal GR24 concentration and temperature for broomrape germination) after being stored in moist conditions ("conditioning") for different durations and temperatures of conditioning respectively (see legend on the figure). The line represents the model fitted to the data. Based on data from Gibot-Leclerc et al. (2004) (Olivia Pointurier 2019 )

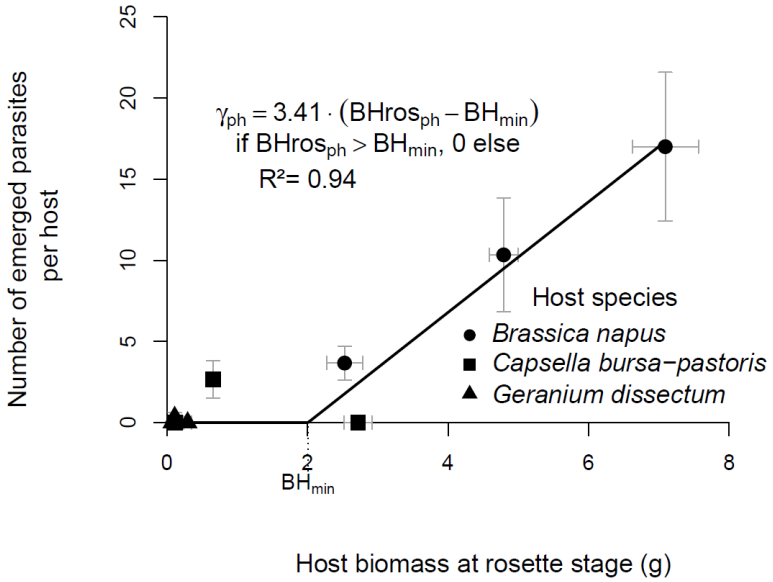

Figure 3: Number of emerged branched broomrapes per host plant (γ_{ph}) surviving until flowering as a function of host biomass at rosette stage ($BHros_{ph}$). Each dot represents the mean value (with bars showing standard deviation) over three independent replicates for a species in a given light condition at rosette stage. The line represents the non-linear model fitted to the data. BH_{min} is the minimum biomass of a host plant at rosette stage to allow the development of broomrapes. Based on data from Moreau et al. (2016) (Olivia Pointurier 2019)

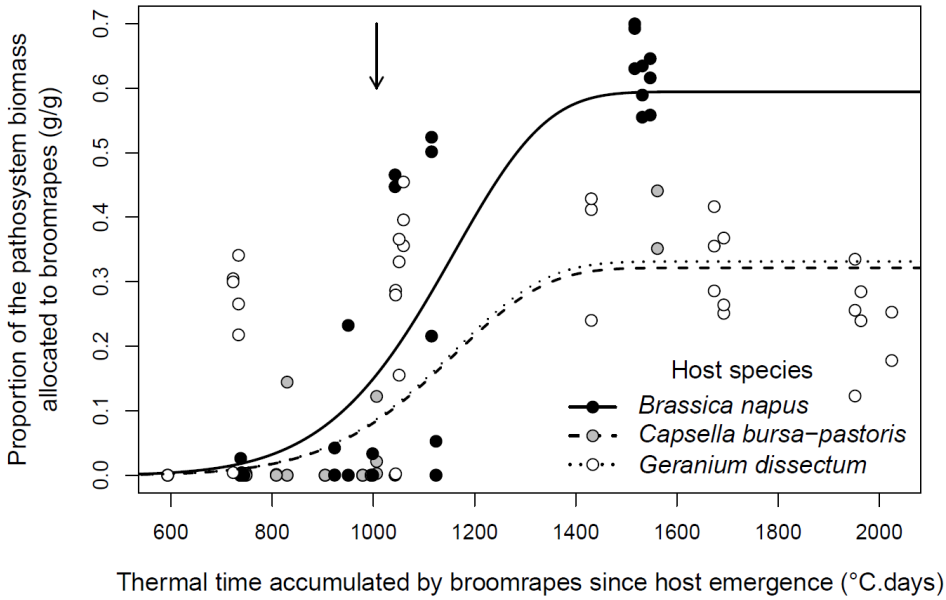

Figure 4: Proportion of the pathosystem biomass (i.e. host + branched-broomrape biomass) allocated to broomrapes over time (thermal time, base 5°C) in three host species. Each dot represents an infected host replicate for a species for one stage and light condition. Lines represent non-linear models fitted for each species. The vertical arrow shows when broomrapes started to emerge. Data from Moreau *et al.* (2016) (Olivia Pointurier 2019)

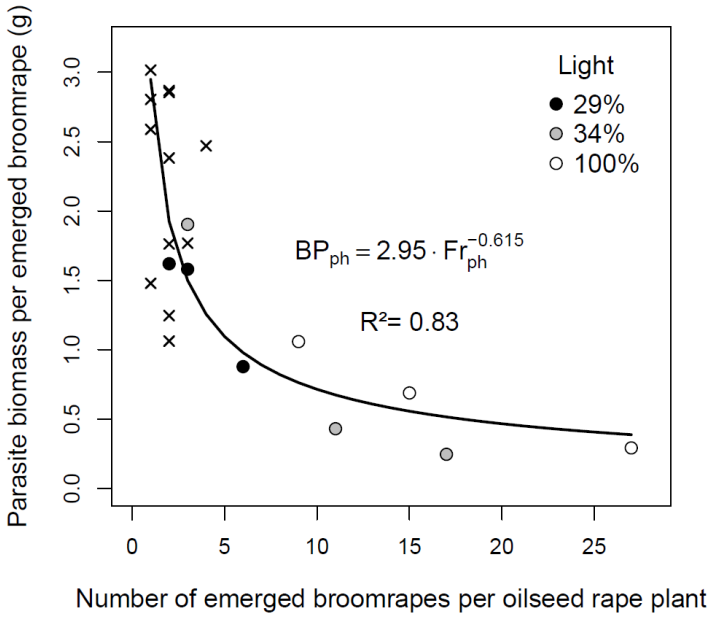

Figure 5: Parasite biomass per emerged branched broomrape (BP_{ph}) as a function of the number of emerged branched broomrapes per oilseed rape plant at host fructification (Fr_{ph}) under greenhouse conditions (dots, Moreau *et al.*, 2016) and in the field (crosses, see section 2.3.2). Each dot represents a replicate of the total biomass of all broomrapes attached on a host divided by the number of flowering broomrapes in one light condition. Each cross is the mean biomass per fructifying broomrape on a host measured in the experimentation described in section 2.3.2. The line represents the non-linear model fitted to the data from Moreau et al. (2016) (dots). (Olivia Pointurier 2019 )

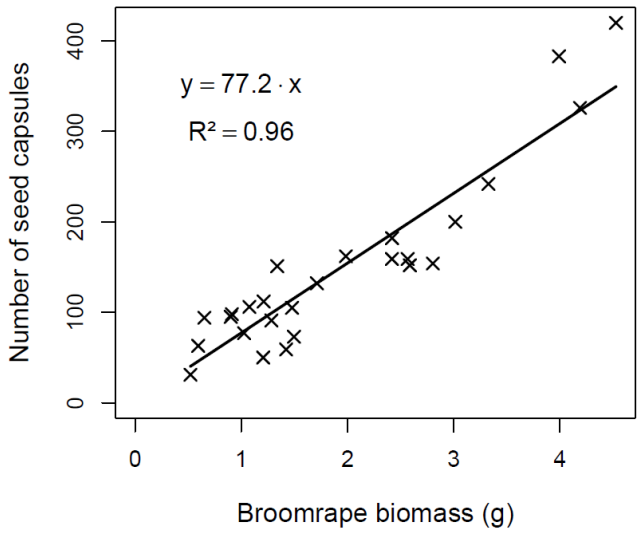

Figure 6: Number of seed capsules produced per branched broomrape as a function of branched broomrape biomass at fructification stage. Each dot represents a measurement on a broomrape collected at maturity from naturally infested fields of winter oilseed rape (see section 2.3.2). The number of capsules includes closed, open and missing capsules. Broomrape biomass was calculated as explained in section 2.3.2 (Olivia Pointurier 2019 )

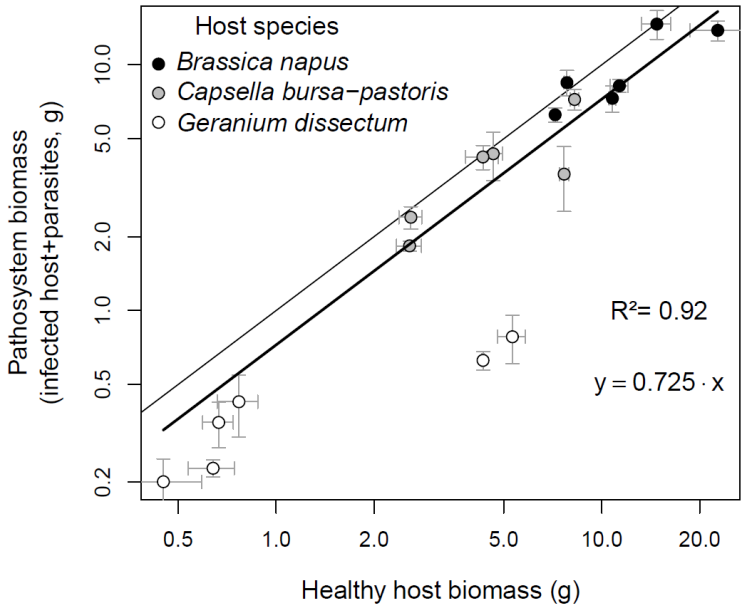

Figure 7: Relationship between the pathosystem biomass (host plant + attached branched broomrapes) of infected and healthy plants for three host species from host flowering onwards. Each dot represents the mean value over three independent replicates for a species at a given stage in a given light condition. Bars represent standard deviations. The thick line represents the linear model fitted to the data, thin line shows y=x. Note the log-log scale. Data from Moreau *et al.* (2016) (Olivia Pointurier 2019 )

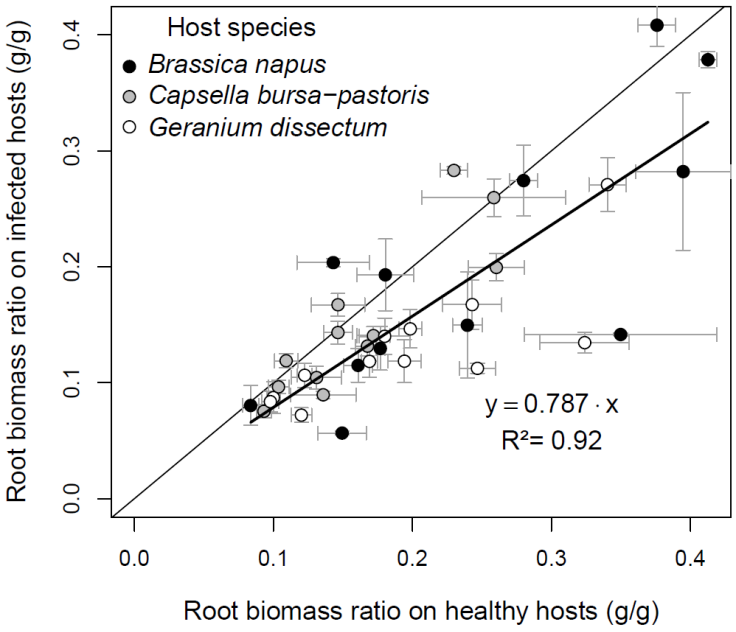

Figure 8: Relationship between the proportions of the pathosystem (host plant + attached branched broomrapes) biomass allocated to roots in infected and healthy plants for three host species from host rosette stage onwards. Root biomass ratio is the host root biomass divided by the total pathosystem biomass. Each dot represents the mean value over three independent replicates for a species at a given stage in a given light condition. Bars represent standard deviations. The thick line represents the linear model fitted to the data, thin line shows y=x. Data from Moreau *et al.* (2016) (Olivia Pointurier 2019 )

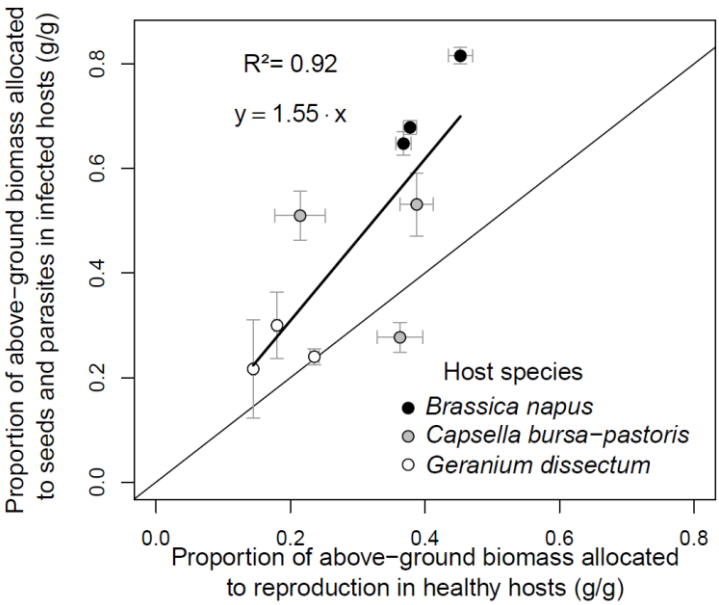

Figure 9: Relationship between the proportions of the above-ground pathosystem (host plant + attached branched broomrapes) biomass allocated to reproduction and branched broomrapes in infected and healthy plants for three host species at host fructification. Each dot represents the mean value over three independent replicates for a species in a given light condition. Bars represent standard deviations. The thick line represents the linear model fitted to the data, thin line shows y=x. Data from (Moreau *et al.*, 2016) (Olivia Pointurier 2019 )

Table 2: Effects of cropping techniques on branched-broomrape dynamics in PHERASYS

Cropping technique	**Effect**	**Consequences on broomrape dynamics**
Tillage	Buries and excavates seeds	Determines the proximity of broomrape seeds to stimulating/attaching roots, and thus the number of germinated seeds/attachments
Crop species and variety	Crop root distribution	Same as tillage
	Broomrape seed stimulation ability	Determines the number of stimulated broomrape seeds
	Broomrape seed attachment ability; host plant biomass	Determines the number of attached broomrape seeds that will survive up to maturity
	Crop plant life duration	Broomrapes die before reproducing if the host dies. Hosts reproducing suffer less from broomrape competition.
	Sowing season	Determines broomrape seed dormancy level when crops stimulate broomrape germination.
Sowing date	Determines crop emergence and life duration	The later broomrape emergence is, the less time there is for broomrapes to damage the crop and to reproduce
Crop sowing density	Number of crop seeds in the soil	Same as tillage
Weed management	Indirect effects via the non-parasitic weed flora (see crop species and variety).	

9 Appendixes

Appendix A 1. Equations of the PHERASYS model representing branched broomrape dynamics and the effect of parasitism on host growth. Meaning of indices: a = seed age class (young vs. old), d = day, l = soil layer, ph = plant p of species h. Parameters are in bold. For explanations on parameters and state variables, see Appendix A 2, Appendix A 3 and Appendix A 4.

Eq.	when	Process	Equation
Broomrape dynamics			
[1]	∀d	Seed mortality	da = 1-(365-**am**·age$_a$)/(365-**am**·(age$_a$-1)) SB$_{lda}$= (1-da)·SB$_{l(d-1)a}$
[2]	∀d If d ∈ [**dFr$_{ph}$,d0**] If Ψ$_{ld}$ ≥ **Ψ$_{min\ cond}$**	Thermal time accumulated during conditioning of fresh seeds	If T$_{ld}$ ∈ [**T$_{min\ cond}$,T$_{opt\ cond}$**] TT$_{cond\ ld}$ = TT$_{cond\ l(d-1)}$ + (T$_{ld}$-**T$_{min\ cond}$**) Else if T$_{ld}$ ∈]**T$_{opt\ cond}$, T$_{max\ cond}$**] TT$_{cond\ ld}$ = TT$_{cond\ l(d-1)}$ + (**T$_{max\ cond}$**-T$_{ld}$) Else if T$_{ld}$ < **T$_{min\ cond}$** or T$_{ld}$ > **T$_{max\ cond}$** TT$_{cond\ ld}$ = TT$_{cond\ l(d-1)}$ + 0
[3]	If age$_a$<**d0** Else	Dormancy release of fresh seeds (conditioning)	If a = young $pND_{lda} = pND'_{lda} \cdot \left[1 - e^{-\ln(2)\left(\frac{TT_{cond\ ld}}{TT_{50\ cond}}\right)^{bprec}}\right]$ pND$_{lda}$ = pND'$_{lda}$
[4]	 If d ∈]**d4$_a$,d1$_a$**] If d ∈]**d1$_a$,d2$_a$**] If d ∈]**d2$_a$,d3$_a$**] If d ∈]**d3$_a$,d4$_a$**] If d >**d4$_a$**	Seasonal dormancy • Low dormancy • Dormancy induction • Dormancy • Dormancy release • Low dormancy	 pND'$_{lda}$ = **ndmax$_a$** pND'$_{lda}$ = **ndmax$_a$**-(d-**d1$_a$**)·(**ndmax-ndmin**)/(**d2$_a$-d1$_a$**) pND'$_{lda}$ = **ndmin** pND'$_{lda}$ = **ndmin**+(d-**d3$_a$**)·(**ndmax -ndmin**)/(**d4$_a$-d3$_a$**) pND'$_{lda}$ = **ndmax**
[5]	If d ∈ [de$_{ph}$,dfle$_{ph}$] ∀ h	Potential root stimulating volume	VS$_{ldph}$ = π·(**d$_{max\text{-}stimu}$** + **rd$_h$/2**)²· RLD$_{ldph}$ with RLD$_{ldph}$ = SRL$_{dph}$ · VSR$_{ldph}$ · RBD$_{ldph}$ · 1000
[6]	If d ∈ [de$_{ph}$,dfle$_{ph}$] If h = stimulating species	Germination triggering	pNDS$_{lda}$ = pND$_{lda}$ · $\sum_h \boldsymbol{\alpha_{h/GR24}}$ [$\sum_p^{N_{dh}}$(VS$_{ldph}$ - VS$_{l(d-1)ph}$)] NDS$_{lda}$ = SB$_{lda}$ · pNDS$_{lda}$
[7]	∀d	Cumulated germination Merging consecutive germination flushes	If HTT$_{ld}$ ≥ x$_0$ $CG_{lda} = NDS_{lda} \cdot \left[1 - e^{-\ln(2)\left(\frac{HTT_{ld}-x_0}{x_{50}-x_0}\right)^{b}}\right]$ If HTT$_{ld}$ < x$_0$ CG$_{lda}$ = 0 If HTT$_{ld}$1 < 2.5 · x$_{501}$ m=min(1; m$_1$+m$_2$) x$_0$=(m$_1$·x$_{01}$ + m$_2$·max(x$_{02}$;HTT$_{ld1}$))/m x$_{50}$=(m$_1$·x$_{501}$ + m$_2$· (x$_{502}$+HTT1$_{ld1}$))/m b=b$_1$+b$_2$ HTT$_{ld}$=HTT$_{ld1}$
[8]	∀d	Hydrothermal time accumulated since the first triggering in the current moist period, following the merging of germination flushes	If T$_{ld}$ ≥ **T$_{base}$** and Ψld ≥ **Ψ$_{base}$** HTT$_{ld}$ = HTT$_{l(d-1)}$ + (T$_{ld}$-**T$_{base}$**)·(Ψ$_{ld}$-**Ψ$_{base}$**)/ (Ψ$_{opt}$-**Ψ$_{base}$**) If T$_{ld}$ < **T$_{base}$** and Ψld ≥ **Ψ$_{base}$** HTT$_{ld}$ = HTT$_{l(d-1)}$ + 0 If Ψ$_{ld}$ < **Ψ$_{base}$** or if tillage which dilutes root exudates HTT$_{ld}$ = 0
[9]	∀d	Daily number of germinated seeds	G$_{lda}$ = CG$_{lda}$ – CG$_{l(d-1)a}$ SB$_{lda}$' = SB$_{lda}$ - G$_{lda}$
[10]	∀d If h = host species	Attachment zone around stimulating roots	VF$_{ldph}$ = π·(**d$_{max}$**+ **rd$_h$**/2)²·RLD$_{ldph}$
[11]	∀d If h = host species	Total attachments on all host plants (before competition between attachments for host ressources)	F$_{ld}$ = (G$_{ld\ young}$ + G$_{ld\ old}$) · $\sum_p VF_{ldph}$
[12]	∀d If h = host species	Attachments on individual host plants (before competition	F$_{ldph}$ = F$_{ld}$ · VF$_{ldph}$ / $\sum_p VF_{ldph}$

Eq.	when	Process	Equation
Broomrape dynamics			
		between attachments for host ressources)	
[13]	If d = $dros_{ph}$ If h = host species	Host carrying capacity	If $BHros_{ph} \leq \mathbf{BH_{min}}$ $\gamma_{ph} = 0$ Else $\gamma_{ph} = \boldsymbol{\delta}\cdot(BHros_{ph} - \mathbf{BH_{min}})$ If $\gamma_{ph} \geq 20$ $\gamma_{ph} = 20$
[14]	If d = $dros_{ph}$ If h = host species	Cumulated attachments at host rosette stage	$Fros_{ph} = \sum_{de_{ph}}^{dFr_{ph}} \sum_l F_{ldph}$
[15]	If d = $dros_{ph}$ If h = host species	Competition between attachments at host rosette stage	If $\gamma_{ph} > 0$ $Fr_{dph} = \gamma_{ph}\cdot(1\text{-}e^{-Fros_{ph}/\gamma_{ph}})$ Else $Fr_{dph} = 0$
[16]	If d > $dros_{ph}$ If h = host species	Competition between attachments after host rosette stage	If $\gamma_{ph} > 0$ $\Delta FS_{dph} = \left(e^{-\sum_l F_{ldph}/\gamma_{ph}}\right) \cdot \sum_l F_{ldph}$ Else $\Delta FS_{dph} = 0$
[17]	If d∈] $dros_{ph,}$ dFr_{ph}] If h = host species	Total number of attached broomrapes	$Fr_{dph} = Fr_{d\text{-}1ph} + \Delta FS_{dph}$
[18]	If d∈] $dros_{ph,}$ dFr_{ph}] If h = host species	Total number of attached broomrapes	If host p dies $Fr_{dph} = 0$
[19]	If d∈] $dros_{ph,}$ dFr_{ph}] If h = host species	Broomrape biomass at seed shed	$BP_{ph} = \mathbf{b1} \cdot Fr_{ph}^{\mathbf{b2}}$
[20]	If d ≥ de_{ph} If h = host species	Thermal time accumulated by broomrape since host emergence	If $T_d \geq T_{base}$ $TT_{ldph} = TT_{l(d\text{-}1)ph} + (T_d\text{-}T_{base})$ If $T_d < T_{base}$ $TT_{ldph} = TT_{l(d\text{-}1)ph} + 0$ dFr_{ph} = first day when $TT_{ldph} \geq 1709$ °C·days
[21]	If d ≥ $dros_{ph}$ If h = host species	Total broomrape biomass on a host over time	$BPT_{dph} = BP_{ph} \cdot Fr_{ph} \cdot \left[1 - e^{-\ln(2)\left(\frac{TT_{ldph}}{\boldsymbol{TT_{50\,BP}}}\right)^{\boldsymbol{b_{BP}}}}\right]$ $BPT_{dph} = \min(BPT_{dph}, ABH_{phd})$
[22]	If d=dFr_{ph} If h = host species	Broomrape seed production	$NC_{ph} = \mathbf{c}\cdot BPT_{dph}\cdot(1\text{-}\mathbf{ci})$ $SP_{ph} = NC_{ph} \cdot \mathbf{CW}\ /\mathbf{SW}\cdot \mathbf{v}$
[23]	If d=dFr_{ph} If h = host species	Seed return to seed bank	$SB_{ld\ young} = (SB_{l\ young}' + \sum_p SP_{ph})$ with l=0
Effect of parasitism on host growth			
[24]	∀d If h = host species	Effect of parasitism on host growth	If d ≥ $dflb_{ph}$ and $\sum_{de_{ph}}^{dFr_{ph}} \sum_l F_{ldph} > 0$ $BH_{phd} = BH_{ph\ d\text{-}1} + \Delta BH_{phd} \cdot \mathbf{rBH}$ Else $BH_{phd} = BH_{ph\ d\text{-}1} + \Delta BH_{phd}$
[25]	∀d If h = host species	Effect of parasitism on biomass allocation in host roots	If d ≥ $dros_{ph}$ and $\sum_{de_{ph}}^{dFr_{ph}} \sum_l F_{ldph} > 0$ $RBH_{phd} = RBH_{phd\text{-}1} + \Delta BH_{phd} \cdot \mathbf{rBH} \cdot RBR_{ph} \cdot \mathbf{rRBH}$ Else $RBH_{phd} = RBH_{phd\text{-}1} + \Delta BH_{phd} \cdot RBR_{ph}$
[26]	∀d If h = host species	Effect of parasitism on biomass allocation in host above-ground organs	$ABH_{phd} = BH_{phd} - RBH_{ph}$ $LBH_{phd} = LBR_{phd} \cdot ABH_{phd}$
[27]	If $stage_p$=seed production If h = host species	Seed production in healthy hosts	$SeBHh_{phd} = \mathbf{HI_s} \cdot ABH_{phd}^{\boldsymbol{bHI_s}}$
[28]	If $stage_p$=seed production If h = host species	Biomass allocation to seeds and broomrapes in infected hosts	If $\sum_{de_{ph}}^{dFr_{ph}} \sum_l F_{ldph} > 0$ $SHPB_{phd} = SeBHh_{phd} \cdot \mathbf{rSPBH}$
[29]	If $stage_p$=seed production If h = host species	Seed production in infected hosts	If $SHPB_{phd} > BPT_{dph}$, $SeBHp_{phd} = SHPB_{phd} - BPT_{dph}$ Else $SeBHp_{phd} = 0$

Appendix A 2. Parameters used in PHERASYS. Parameters specific to host species (rd_h and $\alpha_{h/GR24}$) are listed in Appendix A 4.

Para-meter	Meaning and unit	Estimated value	
		Oilseed rape pathovar	**Hemp pathovar**
am	Annual mortality rate of broomrape seeds (in $year^{-1}$)	0.0689 ± 0.0107	0.0418 ± 0.00795
b	Shape parameter in the equation modelling germination dynamics of broomrape seeds	1.72 ± 1.73*	2.58 ± 1.64*
b1	Coefficient relating broomrape biomass per individual to the number of broomrapes per host plant (in $g \cdot g^{-1}$)	2.95 ± 0.527	NA
b2	Coefficient relating broomrape biomass per individual to the number of broomrapes per host plant (no unit)	-0.615 ± 0.127	NA
b_{BP}	Shape parameter in the equation modelling broomrape biomass accumulation over time	7.40 ± 2.57	NA
b_{cond}	Shape parameter in the equation modelling conditioning of fresh seeds	1.80 ± 1.70	NA
BH_{min}	Minimum biomass of a host plant at rosette stage to allow the development of broomrapes (in g)	2.01 ± 0.368	NA
c	Number of seed capsules per gram of broomrape (in g^{-1})	7.72 ± 3.20	NA
ci	Proportion of broomrape seed capsules that will not produce mature seeds (capsules with immature seeds, eaten by insects or atrophied)	0.0848	NA
CW	Mean weight of broomrape seeds per capsule (in g)	$5.49 \cdot 10^{-4} \pm 8.18 \cdot 10^{-5}$*	NA
d0	Date of dormancy release of fresh broomrape seeds (in julian days)	First day when $TT_{cond\ ld} \geq 250$ °C·days	NA
$d1_a$	Date of seasonal dormancy induction onset (in julian days) for - Young seeds - Old seeds	 267 ± 0.00 + 61 ± 11.1	 NA NA
$d2_a$	Date of seasonal dormancy induction end (in julian days) for - Young seeds - Old seeds	 5 ± 14.4 + 61 ± 11.1	 NA NA
$d3_a$	Date of seasonal dormancy release onset (in julian days) for - Young seeds - Old seeds	 113 ± 3.23 + 61 ± 11.1	 NA NA
$d4_a$	Date of seasonal dormancy release end (in julian days) for - Young seeds - Old seeds	 122 ± NA + 61 ± 11.1	 NA NA
dFr_{ph}	Date of fructification of broomrape (in degree-days, base 5°C, days since host emergence)	1709°C·days ***	NA
d_{max}	Maximum distance from a stimulating root for broomrape seeds to attach to the root (in m)	0.004**	
$d_{max\text{-}stimu}$	Maximum distance from a stimulating root for broomrape seeds to perceive germination stimulants (in m)	0.036**	
ndmax	Maximum proportion of non-dormant broomrape seeds	0.911 ± 0.0334	NA
ndmin	Minimum proportion of non-dormant broomrape seeds	0.159 ± 0.0448	NA
rBH	Rate of biomass reduction due to parasitism in the pathosystem (host + attached broomrapes, in $g^1 \cdot g^{-1}$)	0.725 ± 0.0497	NA
rRBH	Rate of reduction in biomass allocation to roots due to parasitism in the pathosystem p (host p + attached broomrapes, in $g^2 \cdot g^{-2}$)	0.787 ± 0.0397	NA
rSPBH	Proportion of healthy reproductive compartment allocated to host seeds and broomrapes in the pathosystem (host + attached broomrapes, in $g^2 \cdot g^{-2}$)	1.55 ± 0.148	NA
SW	Mean weight of a broomrape seed (in g)	$2.09 \cdot 10^{-6} \pm 2.63 \cdot 10^{-7}$*	$5.41 \cdot 10^{-6}$
T_{base}	Base temperature for germination of broomrape seeds (in °C)	5**	NA

Para-meter	Meaning and unit	Estimated value	
		Oilseed rape pathovar	Hemp pathovar
$T_{max\ cond}$	Maximum temperature for conditioning of broomrape seeds (in °C)	36.7 ± 3.55	NA
$T_{min\ cond}$	Minimum temperature for conditioning of broomrape seeds (in °C)	0.00 ± 3.17	NA
$T_{opt\ cond}$	Optimum temperature for conditioning of broomrape seeds (in °C)	18.0 ± 2.67	NA
$TT_{50\ BP}$	Thermal time accumulated by broomrape from host emergence up to 50% of the total broomrape biomass is reached (in °C.days)	1130 ± 40.3	NA
$TT_{50\ cond}$	Thermal time when 50% of fresh broomrape seeds are conditioned (in °C·days)	70.0 ± 10.7	NA
v	Proportion of viable broomrape seeds at seed shed	0.933 ± 0.0185*	0.927 ± 0.0158*
x_0	Hydrothermal time from germination triggering to first germinated broomrape seeds (in °C·MPa·MPa^{-1}·days)	57.9 ± 34.4*	39.4 ± 21.2*
x_{50}	Hydrothermal time from germination triggering to 50% of final germination of broomrape seeds (in °C·MPa·MPa^{-1}·days)	98.3 ± 50.2*	61.9 ± 18.0*
δ	Maximum number of attached broomrapes supported per gram of plant p at rosette stage (in g^{-1})	3.41 ± 0.428	NA
Ψ_{base}	Base water potential for germination of broomrape seeds (in MPa)	-3.5**	NA
$\Psi_{min\ cond}$	Minimum water potential for conditioning of broomrape seeds (in MPa)	-2	NA

Parameters are estimated by linear or non-linear regressions (parameter value **±** standard error)**,** or by calculating mean values ± standard deviation (*) or from the literature (** (Gibot-Leclerc *et al.*, 2004) ***(Gibot-Leclerc, 2004)).

Appendix A 3: Name, meaning and unit of variables in PHERASYS. Meaning of indices: a = seed age class (young vs. old), d = day, l = soil layer, ph = plant p of species h.

Variable	Meaning	Unit	Predic-ted by	
ABH_{phd}	Above-ground biomass of the pathosystem p (including attached broomrapes in infected hosts) (Colbach *et al.*, 2014b)	g·host^{-1}	x	
age_a	Broomrape seed age	days		x
BH_{phd}	Pathosystem (=host p + attached broomrapes) biomass on day d	g·host^{-1}	x	x
$BHros_{ph}$	Biomass of infected host plant p at rosette stage	g	x	
BP_{ph}	Biomass of each broomrape at fructification stage on host plant p	g·broomrape^{-1}		x
BPT_{dph}	Total broomrape biomass on host plant p on day d	g·host^{-1}		x
CG_{lda}	Cumulated number of germinated broomrape seeds in soil layer l on day d	seeds·m^{-2}		x
Da	Daily seed mortality rate of broomrape seeds (Gardarin *et al.*, 2012)	days^{-1}		x
de_{ph}	Emergence date of the stimulating plant p	Julian days	x	
$dflb_{ph}$	Date of beginning of flowering of host plant p	Julian days	x	
$dfle_{p}$	Date of end of flowering of the stimulating plant p	Julian days	x	
$dros_{ph}$	Date when host plant p reaches rosette stage	Julian days	x	
F_{ld}	Total number of attachments among germinated broomrape seeds in soil layer l before competition between attachments for host resources	Attachments ·host^{-1}		x
F_{ldph}	Number of attachments on roots of host plant p in soil layer l before competition between attachments for host resources	Attachments ·host^{-1}		x

Variable	Meaning	Unit	Predicted by	
$Fros_{ph}$	Total number of broomrapes attached on host plant p at rosette stage before competition between attachments for host resources	Attachments ·host^{-1}		x
Fr_{ph}	Total number of broomrapes attached on host plant p on day d	Broomrapes ·host^{-1}		x
G_{lda}	Density of germinated broomrape seeds	seeds·m^{-2}		x
HTT_{ld}	Hydrothermal time accumulated by broomrape seeds in soil layer l on day d since germination triggering by root exudates	°C·MPa·MPa^{-1} ·days		x
LBH_{phd}	Leaf biomass of host plant p (Colbach *et al.*, 2014b)	g·host^{-1}	x	
LBR_{phd}	Leaf vs. above-ground biomass ratio in host plant p (Colbach *et al.*, 2014b)	g·g^{-1}	x	
NC_{ph}	Number of seed capsules produced per attached broomrape on host plant p	broomrape^{-1}		x
N_{dh}	Density of plants of species h stimulating broomrape germination	plants·m^{-2}		x
NDS_{lda}	Density of non-dormant broomrape seeds stimulated by root exudates	seeds·m^{-2}		x
pND'_{lda}	Proportion of non-dormant broomrape seeds over seasons (before conditioning in case of fresh seeds)	seeds·seeds^{-1}		x
pND_{lda}	Proportion of non-dormant broomrape seeds	seeds·seeds^{-1}		x
$pNDS_{lda}$	Proportion of non-dormant broomrape seeds stimulated by root exudates of all stimulating plants in soil layer l	seeds·seeds^{-1}		x
RBD_{ldph}	Root biomass density of stimulating plant p in soil layer l (Pagès *et al.*, 2020)	g·dm^{-3}	x	
RBH_{phd}	Root biomass of host plant p	g·host^{-1}	x	x
RBR_{ph}	Proportion of biomass allocated to roots in healthy plant p (Pointurier *et al.*, submitted)	g·g^{-1}	x	
RLD_{ldph}	Cumulated root length density of stimulating plant p in soil layer l	m·m^{-2}	x	
SB_{lda}	Density of viable broomrape seeds in soil layers	seeds·m^{-2}		x
SB_{lda}'	Density of viable broomrape seeds after germination losses	seeds·m^{-2}		x
$SeBHh_{phd}$	Seed biomass in healthy plants p (Colbach *et al.*, 2014b)	g·host^{-1}	x	
$SeBHp_{phd}$	Host seed biomass in infected host plant p	g·host^{-1}		x
$SHPB_{phd}$	Biomass allocated to host seeds and attached broomrapes in the pathosystem p (=host p + attached broomrapes)	g·host^{-1}		x
SP_{ph}	Number of viable broomrape seeds produced on host plant p	host^{-1}		x
SRL_{dph}	Specific root length of stimulating plant p (Pagès *et al.*, 2020)	m·g^{-1}	x	
T_d	Daily mean air temperature	°C	input	
T_{ld}	Daily mean soil temperature in layer l	°C	x	
$TT_{cond\ ld}$	Thermal time accumulated by broomrape seeds since they were released from the mother plant	°C·days		x
TT_{ldph}	Thermal time accumulated by broomrape since host plant p emerged	°C·days		x
VF_{ldph}	Proportion of soil volume in layer l where broomrape seeds are close enough to the roots of host plant p to attach it	m^3·m^{-3}		x
VS_{ldph}	Proportion of soil volume in layer l permeated with germination stimulants exuded by roots of plant p	m^3·m^{-3}		x
VSR_{ldph}	Proportion of soil volume in layer l occupied by the root system of stimulating plant p (Pagès *et al.*, 2020)	m^3·m^{-3}	x	
γ_{ph}	Maximum number of broomrapes supported by host plant p	Attachments ·host^{-1}		x
ΔBH_{phd}	New biomass produced by host plant p on day d through photosynthesis after deduction of respiration loss (Colbach *et al.*, 2014b)	g·host^{-1}	x	
ΔFS_{dph}	Daily number of broomrapes attached on host plant p after host rosette stage	Attachments ·host^{-1}		x
Ψ_{ld}	Daily water potential in soil layer l	MPa	x	

Appendix A 4. Crop and weed parameters characterizing interaction with branched broomrape. In case of missing data, data from a close species (*), from another pathovar (**) or from number of attachments instead of germination rate for $\alpha_{h/GR24}$ (***, section 3.1.3) were used. Root tip diameters originate from parameters of the root architecture model ArchiSimple (Pagès *et al.*, 2014, Pagès, pers. comm.; Moreau *et al.*, 2017; Seneze, 2018; Guinet, 2019). When it was unknown, the mean diameter calculated over all other species was used.

Species	Ability to stimulate broomrape germination relative to GR24 ($\alpha_{h/GR24}$)	Ability to support broomrape development	Root tip diameter (rd_h, in mm)	Reference for stimulating activity and host status[§]
Oat (*Avena sativa*)	0.125**	No**	NA	8 21
Small oat (*Avena strigosa*)	0.125*	No*	NA	Same as oat
Beet (*Beta vulgaris*)	0	No	NA	8 18 19 23
Wheat (*Triticum aestivum*)	0	No	0.802	18 19 23
Oilseed rape (*Brassica napus*)	0.656	Yes	0.377	2 3 8 10 11 13 14 21 24
Fenugreek (*Trigonella foenum-graecum*)	0.307**	Yes**	0.656	8 18 19
Faba bean (*Vicia faba*)	0.443**	No	0.819	8 9 19 21
Chickling pea (*Lathyrus sativus*)	0.00247*	Yes	NA	8 18 19
Field bean (*Phaseolus vulgaris*)	0.00388**	No**	0.519	1 23
Lentil (*Lens culinaris*)	0.0549**	Yes	0.511	1 8 18 19 21
Lens nigricans	0.0549*	Yes*	0.511	Same as lentil
Flax (*Linum usitatissimum*)	0.399**	No	NA	1 8 18 19 21
Birdsfoot trefoil (*Lotus corniculatus*)	1.59	No	NA	21 22
Lucerne (*Medicago sativa*)	0.0154*	No	NA	4 19 21 22
Maize (*Zea mays*)	0.450**	No	0.965	8 9 19 21 23 26
Black medick (*Medicago lupulina*)	0.0154	No*	NA	22
White mustard (*Sinapis alba*)	0.654*	Yes	NA	8 18 19 21
Niger (*Guizotia abyssinica*)	0	No	NA	18 19 21
Barley (*Hordeum vulgare*)	0	No	NA	8 18 19 23
Phacelia (*Phacelia tanacetifolia*)	0	No	NA	18 19
Winter pea (*Pisum sativum*)	0	No	0.751 to 0.758 depending on pea genotypes	1 8 9 18 19 23
Spring pea (*Pisum sativum*)	0	No	0.528	1 8 9 18 19 23
Potato (*Solanum tuberosum*)	0.219***	Yes**	NA	21
Radish (*Raphanus sativus*)	0.507*	No**	NA	23
Soybean (*Glycine max*)	0	No	0.720	1 18 19
Sorghum (*Sorghum bicolor*)	0	No	NA	8 18 19 23
Sunflower (*Helianthus annuus*)	0.443**	Yes	0.535	8 9 19 21 24
Berseem clover (*Trifolium alexandrinum*)	0.0224*	Yes	NA	8 18 19
White clover (*Trifolium repens*)	0.0399	No	NA	16 18 19
Red clover (*Trifolium pratense*)	0.00487	No	NA	19
Triticale (x *Triticosecale*)	0.470**	No	NA	8 19
Common vetch (*Vicia sativa*)	0.00513*	Yes	0.466	8 19
Abutilon theophrasti	No data in the literature			
Aethusa cynapium	NA	Yes	NA	5
Alopecurus myosuroides	0	No	0.418	24
Amaranthus retroflexus	0	No	0.541	23
Ambrosia artemisiifolia	No data in the literature			
Ammi majus	0.267***	Yes	NA	4 24
Anagallis arvensis	0.176***	No	NA	3 24
Arabidopsis thaliana	0.881	Yes	NA	2 4 15 16 17 24 25
Avena fatua	0	No	0.604	24

Species	Ability to stimulate broomrape germination relative to GR24 ($\alpha_{h/GR24}$)	Ability to support broomrape development	Root tip diameter (rd_h, in mm)	Reference for stimulating activity and host status[§]
Bromus sterilis	0	No	0.407	[24]
Capsella bursa-pastoris	0.0467	Yes	0.316	[11 15 16 20 24]
Cyanus segetum	NA	Yes	0.454	[24]
Chenopodium album	0	No	0.474	[3 4]
Datura stramonium	0.0386***	No	NA	[3]
Digitaria sanguinalis	NA	No	NA	[3 24]
Echinochloa crus-galli	0	No	0.640	[3 4]
Euphorbia helioscopia	0.137***	Yes	NA	[11]
Galium aparine	2.50***	Yes	0.343	[3 4 24]
Geranium dissectum	0.481***	Yes	0.333	[4 11 24]
Lapsana communis	1.18***	No	NA	[3 4]
Lolium multiflorum	0	No	NA	[11 19 21 24]
Matricaria chamomilla	0.0394***	Yes	0.406	[23 24]
Tripleurospermum inodorum	0.0394***	Yes	0.406	[24]
Mercurialis annua	0.137***	Yes	NA	[4 11]
Panicum miliaceum	0	No	NA	[23]
Papaver rhoeas	0.137***	Yes	NA	[11 24]
Poa annua	No data in the literature			
Polygonum aviculare	NA	Yes	0.363	[3 11]
Fallopia convolvulus	NA	Yes	0.480	[4]
Persicaria maculosa	0	No	0.431	[3]
Raphanus raphanistrum	0.507	Yes	NA	[3 4 11 16 24]
Senecio vulgaris	0.381***	Yes	0.411	[3 4]
Setaria viridis	NA	No	NA	[24]
Sinapis alba	0.654*	Yes	NA	[8 18 19 21]
Sinapis arvensis	0.654	No	NA	[11 15 16 24]
Solanum nigrum	3.28***	No	0.583	[3 4]
Sonchus asper	2.26***	Yes	0.429	[3 4 12 24]
Stellaria media	0	No	0.329	[3]
Veronica hederifolia	0.0427*	Yes	0.286	[24]
Veronica persica	0.0427***	Yes*	NA	Same as *V. hederifolia*
Viola arvensis	NA	Yes	NA	[24]

[§] References are (sorted alphabetically):

[1] (Arslan and Uygur, 2013);
[2] (Auger *et al.*, 2012)
[3] (Boulet *et al.*, 2001)
[4] (Boulet *et al.*, 2007)
[5] (Boulet *et al.*, 2013)
[6] (Brault *et al.*, 2007)
[7] (Denev *et al.*, 2007)
[8] (Fernández-Aparicio *et al.*, 2009)
[9] (Fernández-Aparicio *et al.*, 2011)
[10] (Gauthier *et al.*, 2012)
[11] (Gibot-Leclerc *et al.*, 2003)
[12] (Gibot-Leclerc, 2004)
[13] (Gibot-Leclerc *et al.*, 2012)
[14] (Gibot-Leclerc *et al.*, 2013b)
[15] (Gibot-Leclerc *et al.*, 2015)
[16] (Gibot-Leclerc *et al.*, 2016)
[17] (Goldwasser and Yoder, 2001)
[18] (Jestin *et al.*, 2014)
[19] (Molenat *et al.*, 2013)
[20] (Moreau *et al.*, 2016)
[21] (Parker and Riches, 1993)
[22] (Perronne *et al.*, 2017)
[23] (Qasem and Foy, 2007)
[24] (Simier *et al.*, 2013)
[25] (Westwood, 2000)
[26] (Zehhar *et al.*, 2003)